



Dental development in living and fossil orangutans



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ABSTRACT

Numerous studies have investigated molar development in extant and fossil hominoids, yet relatively little is known about orangutans, the only great ape with an extensive fossil record. This study characterizes aspects of dental development, including cuspal enamel daily secretion rate, long-period line periodicities, cusp-specific molar crown formation times and extension rates, and initiation and completion ages in living and fossil orangutan postcanine teeth. Daily secretion rate and periodicities in living orangutans are similar to previous reports, while crown formation times often exceed published values, although direct comparisons are limited. One wild Bornean individual died at 4.5 years of age with fully erupted first molars (M1s), while a captive individual and a wild Sumatran individual likely erupted their M1s around five or six years of age. These data underscore the need for additional samples of orangutans of known sex, species, and developmental environment to explore potential sources of variation in molar emergence and their relationship to life history variables. Fossil orangutans possess larger crowns than living orangutans, show similarities in periodicities, and have faster daily secretion rate, longer crown formation times, and slower extension rates. Molar crown formation times exceed reported values for other fossil apes, including *Gigantopithecus blacki*. When compared to African apes, both living and fossil orangutans show greater cuspal enamel thickness values and periodicities, resulting in longer crown formation times and slower extension rates. Several of these variables are similar to modern humans, representing examples of convergent evolution. Molar crown formation does not appear to be equivalent among extant great apes or consistent within living and fossil members of *Pongo* or *Homo*.

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1. Introduction

Hominins and orangutans are represented by fossil records with substantial regional and temporal diversity, which has important implications for understanding the appearance and evolution of both taxa. The two living orangutan species (*Pongo pygmaeus* and *Pongo abelii*, from Borneo and Sumatra, respectively) appear to have diverged between 0.4 and 5 million years ago (Xu and Arnason, 1996; Zhang et al., 2001; Steiper, 2006; Arora et al., 2010; Locke et al., 2011), and their fossil record extends back into the early Pleistocene of mainland Asia (reviewed in Drawhorn, 1995; Cameron, 2001; Smith et al., 2011; Harrison et al., 2014). Several fossil orangutan species and subspecies have been recognized, largely on the basis of dental metric variation, occlusal morphology, and geographical location. It is clear that fossil *Pongo* dentitions are larger and more variable than modern populations (Hooijer, 1948;

Schwartz et al., 1995; Bacon and Long, 2001; Cameron, 2001). Fossil orangutans show greater average enamel thickness than living orangutans, which is significantly different in comparisons of first molars (M1s; Smith et al., 2011). One aspect of incremental tooth growth, the long-period line periodicity, was reported to be similar to living species (Hu et al., 2012). However, nothing is known about enamel secretion rates or crown formation times, leaving the mechanisms of tooth formation in fossil orangutans largely unknown. This study aims to address these issues by documenting molar crown formation, first in captive and wild orangutans from Borneo and Sumatra, and then in a sample of isolated fossil orangutan (*Pongo* sp.) postcanine teeth from mainland Asia and Indonesia.

Understanding dental development in living and fossil orangutans may also shed light on the evolution of Asian apes and the divergence of the Asian and African lines of great ape and human evolution. Studies of incremental development (daily secretion rate, long-period line periodicities, crown formation times) and/or molar eruption in Miocene hominoids *Proconsul* (Beynon et al.,

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1998; Dean, 2006), *Dryopithecus* (Kelley et al., 2001), *Afropithecus* (Kelley and Smith, 2003; Smith et al., 2003), *Gigantopithecus* (Dean and Schrenk, 2003), *Lufengpithecus* (Schwartz et al., 2003; Zhao et al., 2008), *Graecopithecus* (Smith et al., 2004), *Sivapithecus* (Mahoney et al., 2007), *Kenyapithecus* (Kelley, 2008), *Hispanopithecus* (Dean and Kelley, 2012), and *Oreopithecus* (Zanolli et al., 2016) have begun to provide a comparative context for interpreting the evolution of these characters during the past 20 million years. However, these data are not available for a reasonable sample of orangutans. With the exception of a study of great ape canine formation (Schwartz and Dean, 2001; Schwartz et al., 2001), incremental development and/or molar eruption has been characterized in only four *Pongo* individuals (Brandes, 1939; Beynon et al., 1991a; Kelley and Schwartz, 2010). Previous studies most commonly report enamel daily secretion rate, with fewer presenting long-period line periodicities, observations of long-period line morphology, or crown formation times (e.g., Martin, 1983; Beynon et al., 1991a, b, 1998; Beynon and Reid, 1995; Dean, 1995a, b, 1998a, b, 2000, 2006; Dean and Shellis, 1998; Schwartz and Dean, 2001; Schwartz et al., 2001). Moreover, long-term fieldwork has hinted at a prolonged life history in orangutans relative to other great apes (e.g., Knott, 2001; Wich et al., 2009; van Noordwijk et al., 2013), which may be reflected in aspects of crown growth such as later ages at M1 emergence (Brandes, 1939; Kelley and Schwartz, 2010).

Dean and Wood (1981) conducted a landmark radiographic study of 175 juvenile apes of unknown ages, publishing the first chronology of great ape tooth calcification and eruption. They reported that patterns of dental development did not differ among the three genera (*Gorilla*, *Pan*, *Pongo*). However, in order to build their chronology, they assumed that crown formation times in each genus were similar to one another, that each molar crown formed over 2.5 years, and that crown formation did not overlap in successive molars. Subsequent histological and radiographic data, including novel information on initiation ages, crown formation times, and molar eruption ages, has led to a revision of these assumptions (e.g., Winkler et al., 1991; Beynon et al., 1991a; Anemone et al., 1996; Reid et al., 1998; Schwartz and Dean, 2001; Schwartz et al., 2006; Smith et al., 2007b, 2010a, 2013; Kelley and Schwartz, 2010). Recent studies have revealed considerable development variation within and among great ape genera, complicating broad generalizations and limiting inferences about the ancestral great ape developmental condition. A better understanding of dental development in living and fossil orangutans will complement available data on African apes and strengthen interpretation of developmental trends throughout 15 million years of Eurasian hominoid evolution.

2. Materials and methods

2.1. Sample

The living orangutan sample includes 10 wild shot individuals and two captive individuals of unknown origin (Table 1), which range in developmental stage from a juvenile with recently erupted M1s to an adult with recently erupted and root complete third molars (M3s). Ages at death were determined for four individuals (ZSM 1981/48, MCZ 5290, ZSM 1981/246, ZMB 83508) during this study as detailed below. A total of 219 histological sections of the mesial and distal cusps of 79 molars from the 12 individuals were prepared and analyzed according to established procedures, which have been detailed in previous studies (e.g., Beynon et al., 1991a; Reid et al., 1998; Smith et al., 2007b) and are only briefly reviewed here.

Table 1

Living and fossil orangutan teeth examined in the current study.

Taxon	Accession/Origin	Sex ^a	Teeth
<i>Pongo pygmaeus</i>	ZSM 1981/48	F	11 molars
	ZSM 1981/87	F	12 molars
	MCZ 5290	n/a	2 molars
	ZD.1976.1435	M	3 molars
	ZD.1976.1439	M	3 molars
	ZD.1976.1441	F	4 molars
<i>Pongo abelii</i>	ZD.1976.1444	F	4 molars
	ZSM 1981/246	M	10 molars
	ZSM 1981/248	F	12 molars
Captive <i>Pongo</i>	ZMB 83508	n/a	6 molars
	HT 09-02	n/a	6 molars
	HT 162/166-88 ^b	M	6 molars
Fossil <i>Pongo</i>	Sumatra (Dubois)	n/a	13 postcanine fragments ^c
	China (Apothecaries)	n/a	4 molars ^c
	China (Ganqian Cave)	n/a	2 molars
	Vietnam (Duoi U'Oi Cave)	n/a	1 premolar
	Vietnam (Lang Trang Caves)	n/a	1 molar

^a F = female, M = males, n/a = sex unknown.

^b Originally studied by Beynon et al. (1991a).

^c These isolated teeth derive from multiple individuals.

The fossil orangutan sample includes 33 histological sections of the mesial and distal cusps of 21 isolated teeth from Sumatra and mainland Asia. The Sumatran material consists of 13 postcanine fragments from caves in the Padang Highlands collected during Eugene Dubois' excavations from 1888 to 1890 (Hooijer, 1948). The mainland Asian sample includes one premolar from Duoi U'Oi Cave, Vietnam (dated to 66 kya: Bacon et al., 2008), one molar from the Lang Trang Caves (Long et al., 1996; dated to 145 kya: Ciochon, pers. comm.), two molars from Ganqian (Tubo) Cave, China (dated to 94–220 kya: Shen et al., 2001), and four molars from the Chinese apothecary collections housed at the Institute for Vertebrate Paleontology and Paleoanthropology. This latter unprovenanced material is believed to come from Middle Pleistocene southern Chinese deposits (von Koenigswald, 1982).

2.2. Preparation

All material was initially photographed and molded with Coltene President impression materials. One living individual's dentition was micro-CT scanned prior to physical sectioning as detailed in Smith et al. (2012), and all fossil teeth were micro-CT scanned prior to sectioning as detailed in Smith et al. (2011). The majority of the living orangutan thin sections were prepared at the University of Newcastle, while the fossil teeth were subsequently sectioned at the Max Planck Institute for Evolutionary Anthropology or at Harvard University, leading to slight differences in preparatory regimes. In all cases, a target section plane was marked on each tooth after visual examination, which was then embedded in methylmethacrylate or coated with cyanoacrylate. The tooth was then mounted on an annular saw (Microslice 2, Metals Research Limited; APD1, Logitech) or peripheral saw (Buehler Isomet Low Speed) with dental sticky wax. An initial cut was made with a diamond impregnated saw blade, the tooth was then advanced approximately 1 mm and a second cut was made parallel to the first, resulting in a section approximately 0.7 mm thick.

Each thick section was then visually assessed to determine which side was closer to the ideal plane of section passing through dentine horn tips, and a second section was cut when the remaining block faces preserved a better plane. The section face that was closest to the ideal plane was mounted face up on a slide with dental sticky wax, briefly lapped down (Logitech Precision Lapping and Polishing Machine PM2A, Buehler Ecomet 4000, or

Buehler Ecomet 3) to remove saw marks, then ultrasonicated and finished with a 1-micron diamond particle suspension (Kemet Liquid Diamond or Buehler Micropolish Alumina) on a polishing cloth. The section was ultrasonicated again, dehydrated in an ethanol series, air dried, mounted to a slide with Logitech UV curing resin, and placed under a pressurized device with a UV light source for approximately 24 h. After curing, the section was lapped to an approximate 100-micron thickness, ultrasonicated, and finished with a 1-micron polishing suspension. The section was then ultrasonicated, dehydrated in an alcohol series, cleared in xylene, and a cover slip was mounted with DPX mounting media.

2.3. Incremental development quantification

All thin sections were imaged and quantified with an Olympus BX 51 polarized light microscope, Olympus DP 70 or MicroPublisher 5.0 camera, and analySIS software (Soft Imaging Systems, Inc). Cuspal enamel thickness, enamel daily secretion rate (DSR), and long-period line number and periodicity were determined to estimate crown formation time and extension rate as detailed below. Cuspal enamel thickness was measured on unworn or slightly worn mesial and distal molar cusps as the linear distance between the dentine horn tip and the approximate position of the first long-period (Retzius) line at the tooth surface. Measurements were made on micrographs taken with 4× or 10× objectives, and were supplemented with comparable measurements from micro-CT scans of unworn living and fossil orangutan molars (detailed in Smith et al., 2011, 2012). The Mann–Whitney *U* test was used to compare enamel thickness values between living and fossil orangutans when sample sizes of four or more molar cusps were available.

The enamel DSR was determined from daily line (cross-striation) spacing in each unworn cusp, which was measured with a 40× objective. Cross-striations were defined as light and dark bands that crossed enamel prisms perpendicularly, and other short-period structures (laminations and intradian lines: see Smith, 2006) were avoided. Cuspal enamel was divided into inner, middle, and outer thirds; DSR measurements were made across three successive daily lines in several areas in each third, and means and ranges were calculated. Trends from inner to outer cuspal regions were tested using the Jonckheere–Terpstra test in both living and fossil samples. The Mann–Whitney *U* test was used to compare DSR values between living orangutan species and between living and fossil orangutans. The Kruskal–Wallis test was used to compare DSR values among hominoids.

The long-period line periodicity, or number of daily lines between Retzius lines, was determined between successive long-period lines that clearly met the tooth surface. Where possible, cross-striations were counted over multiple long-period line intervals and average periodicities were determined, as this technique may give a more accurate result than counts within single intervals. In some instances, a single integer could not be determined with confidence, and a range of estimates was recorded. The Mann–Whitney *U* test was used to compare periodicity values between living orangutan males and females, and between living and fossil orangutans.

Cusp-specific crown formation times were calculated by summing estimates of cuspal and lateral (imbricational) enamel formation time. Cuspal enamel formation was determined in one of two ways for each unworn or lightly worn molar cusp. In the majority of cases, the linear cuspal enamel thickness was divided by the average cuspal DSR to yield an “uncorrected” estimate of cuspal formation time (in days). To compensate for the three-dimensional curvature of enamel prisms, this value was multiplied by a correction factor (1.00–1.30) based on the degree of observed

decussation in each cusp, yielding a second “corrected” estimate. Because prisms in hominoid cuspal enamel do not appear to decussate in a spiral arrangement (Tafforeau et al., 2012), an average of the uncorrected and corrected values was used. A second method was applied when minor wear resulted in the loss of more than 5% of the outer enamel. In this case, prisms were tracked from the dentine horn to the first visible long-period line, and prism lengths were divided by local daily secretion rate in segments, which were summed to yield the time of cuspal formation.

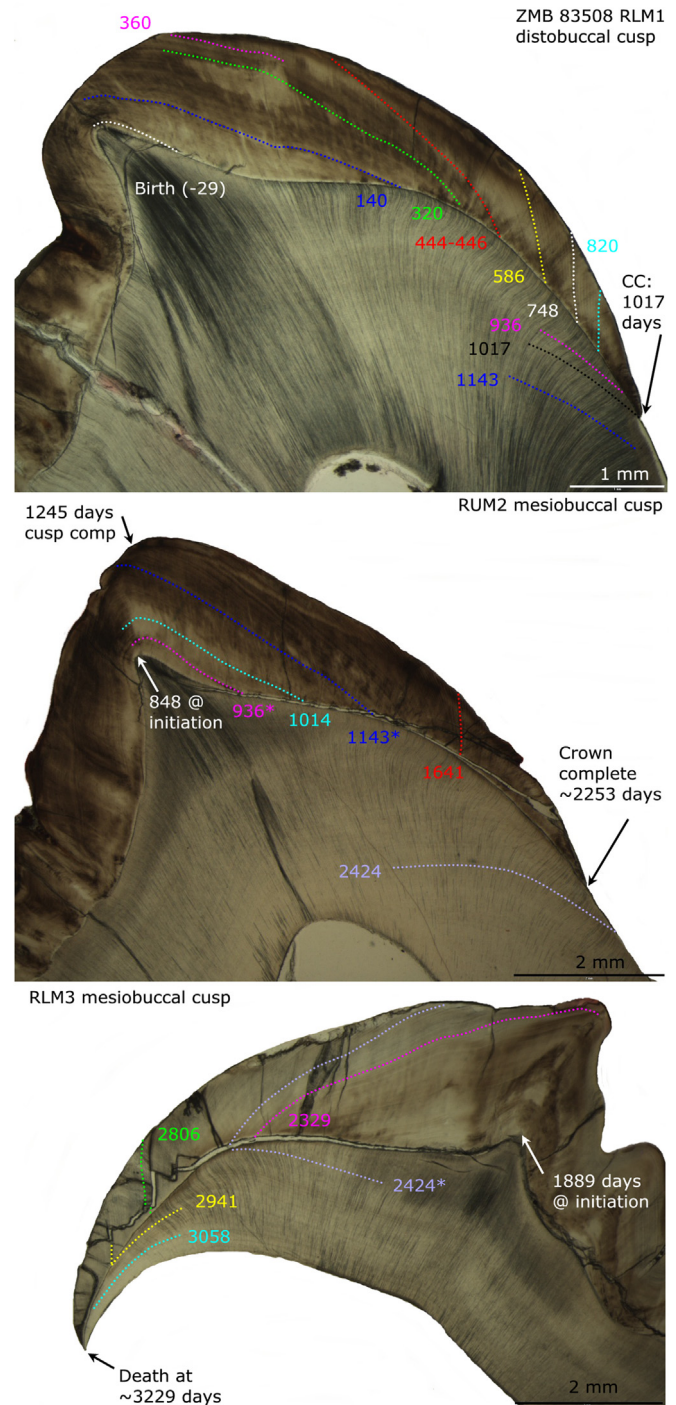


Figure 1. Registry of accentuated lines to establish age at death in a wild-shot Sumatran orangutan (ZMB 83508). Ages followed by an asterisk are accentuated lines used to register successively forming molars.

Correction factors were not applied as areas of marked prism decussation were avoided in these regions lateral to the cusp tip. This approach was also used to estimate the timing of accentuated lines formed after the neonatal (birth) line in order to determine the age at death of four individuals (detailed below.)

Lateral enamel formation was determined as the cusp-specific long-period line number multiplied by the periodicity of that individual. Long-period lines were counted three times from the enamel cervix to the cusp tip for each unworn cusp, and an average was calculated. Slight corrections (<5%) were made when cervical tips were broken or when light wear obscured the first-formed long-period lines in the cuspal region. Cuspal and lateral enamel formation times were then summed to yield the crown formation time, which is specific to each cusp. The cusp-specific extension rate was calculated as enamel–dentine junction (EDJ) length (measured from dentine horn tip to cervix) divided by the crown formation time.

When it was possible to identify the neonatal line in M1s, initiation ages were determined from counts and/or measurements of daily lines. Prism length was measured between the dentine horn tip and the neonatal line, and this was divided by the prenatal DSR to yield the initiation age in days. Age at death was estimated for four individuals by calculation of the postnatal crown formation prior to death. This approach also yielded cusp-specific molar initiation and completion ages. For MCZ 5290, a pair of accentuated lines were matched from the M1 crowns to hypoplasias on the surface of the developing mandibular canine (as in Smith and Boesch, 2015), and subsequent long-period lines (perikymata) were counted in order to capture the entire period of development from birth to death. For ZMB 83508, a series of accentuated lines were identified and registered across the three successively forming molars (as in Smith et al., 2010a; Fig. 1). Several individuals showed complex patterns of accentuated lines, which prohibited conventional approaches to register teeth by matching lines across synchronously-forming regions (as for ZMB 83508 above). Therefore, the elemental mapping approach detailed in Austin et al. (2013, 2016) was used to register molars crowns in ZSM 1981/48 and ZSM 1981/246. Barium banding patterns in the dentine were first matched across successive molars, and these bands were then related to accentuated lines in the enamel. The timing from the initiation of M1 to these registered locations was used to assess their age, and subsequent developmental time was added to determine age at death.

3. Results

Cuspal enamel thickness in living orangutan molars ranged from 0.75 to 2.18 mm depending on the molar and cusp type (Table 2).

Table 2
Cuspal enamel thickness (in microns) in living and fossil orangutans.

Taxon	Tooth	mb	Range (n)	ml	Range (n)	db	Range (n)	dl	Range (n)
Living <i>Pongo</i>	UM1	1175	982–1458 (3)	1054	1000–1108 (2)	1226	900–1595 (3)	n/a	n/a
	UM2	1311	1137–1665 (8)	1684	1369–2180 (7)	1310	1157–1390 (3)	1569	1476–1646 (3)
	UM3	1306	1064–1740 (10)	1655	1184–2145 (10)	1308	1044–1525 (4)	1510	1250–1736 (4)
	LM1	1072	1059–1085 (2)	846	747–994 (4)	1019	– (1)	1287	1103–1510 (5)
	LM2	1445	1306–1584 (2)	1465	1252–1795 (8)	1353	1208–1440 (3)	1492	1291–1661 (8)
	LM3	1561	1031–2020 (7)	1359	844–1952 (13)	1540	1380–1700 (2)	1451	1235–1560 (5)
Fossil <i>Pongo</i>	UM1	1264	1003–1577 (9)	1621	959–2217 (16)	1448	880–1972 (7)	1592	1364–2141 (8)
	UM2	1191	561–1571 (11)	1675	998–2388 (15)	1400	839–1907 (9)	1750	1434–2259 (12)
	UM3	1229	1068–1423 (7)	1717	1422–1956 (11)	1591	1439–1763 (5)	1733	1538–1842 (3)
	LM1	1340	768–1909 (7)	1273	530–1757 (10)	1207	915–1473 (5)	1318	1111–1646 (10)
	LM2	1485	1101–1937 (5)	1432	1161–1748 (8)	1396	– (1)	1570	1485–1647 (4)
	LM3	1472	916–1714 (8)	1444	1230–1767 (13)	1612	1247–1849 (8)	1535	1086–1773 (11)

Tooth: U = upper/maxillary, L = lower/mandibular, M = molar. Cusps: mb = mesiobuccal, ml = mesiolingual, db = distobuccal, dl = distolingual. Average values are given in microns for each cusp, followed by the range and sample size. Measurements were made from histological sections and micro-CT scans of additional unworn living and fossil orangutan molars (detailed in Smith et al., 2011, 2012).

Table 3

Daily secretion rate (in microns/day) in living and fossil orangutan molar cusps.

Taxon	n	Inner	Middle	Outer	Average	St Dev
<i>Pongo pygmaeus</i>	38	3.14	4.05	4.50	3.90	0.33
<i>Pongo abelii</i>	11	3.60	4.23	4.40	4.08	0.31
Captive <i>Pongo</i>	4	3.07	3.92	5.15	4.05	0.18
Living <i>Pongo</i>	53 ^a	3.23	4.08	4.52	3.94	0.33
Fossil <i>Pongo</i>	10	3.60	4.35	4.60 ^b	4.19 ^b	0.26

Inner, middle, and outer refer to regions within the cuspal enamel, and average values reflect the grand mean and standard deviation (St Dev) of these three regions.

^a Living *Pongo* values represent the average of all wild and captive individuals.

^b Based on nine cusps, as the daily lines in one individual were not clear in the outer enamel region.

Cuspal enamel was thicker on M2s and M3s than on M1s, and generally thicker on lingual cusps of maxillary molars than on corresponding buccal cusps. Although Sumatran orangutans showed slightly thicker cuspal enamel in seven of 10 possible comparisons, these values derived from only one to three individuals, prohibiting statistical assessment. Living orangutan cuspal enamel thickness values were lumped for comparison with fossil orangutans, whose cuspal enamel thickness values ranged from 0.53 to 2.39 mm, and also varied among molar and cusp types (Table 2). Average values were slightly greater in fossil orangutans than in the living orangutans, but significant differences were not detected in the 12 comparisons of specific molar cusps represented by four or more individuals.

Enamel daily secretion rate (DSR) was quantified in the cuspal enamel of 53 living orangutan and 10 fossil orangutan molar cusps (Table 3). The Jonckheere–Terpstra test for trends revealed a significant increase in DSR from inner to outer enamel in both living and fossil samples ($p < 0.001$). Sample sizes were too limited to test for differences in regions or overall rates among cusps within a molar type, within cusps among molar types, between buccal and lingual analogues, or between mandibular and maxillary analogues. For subsequent analyses, values were lumped across molar and cusp types because visual inspection did not show consistent trends in DSR among cusps or molar positions, and differences in DSR values were not found among larger samples of chimpanzee molar cusps (Smith et al., 2007b). Comparisons between living species revealed that Sumatran orangutans have significantly greater inner DSR values, but rates do not differ in other regions or overall (Table 4). Living orangutan values were combined for subsequent comparisons with the fossil sample. Fossil orangutans show significantly greater inner DSR values than living orangutans, but DSR does not differ in the middle or outer enamel (Table 4). The average cuspal DSR in fossil orangutans (4.19 microns/day) is

Table 4
Mann–Whitney *U* test comparisons of cuspal daily secretion rate.

Comparison	Inner		Middle		Outer		Average	
	<i>Z</i>	<i>p</i>	<i>Z</i>	<i>p</i>	<i>Z</i>	<i>p</i>	<i>Z</i>	<i>p</i>
Bornean vs. Sumatran	–3.344	<i>0.001</i>	–0.527	0.598	–0.851	0.395	–1.486	0.137
Living vs. Fossil	–2.361	<i>0.018</i>	–1.919	0.055	–0.450	0.653	–1.949	0.051

Inner, middle, and outer refer to regions within the cuspal enamel. Italicized *p*-values indicate significant differences.

Table 5
Long-period line periodicities (in days) in living and fossil orangutans.

Taxon	<i>n</i>	Average	Range
<i>Pongo pygmaeus</i>	7	9.6	9–10
<i>Pongo abelii</i>	3	9.3	9–10
Captive <i>Pongo</i>	2	9.5	9–10
Living <i>Pongo</i>	12 ^a	9.5	9–10
Fossil <i>Pongo</i>	15	10.1	9–12

All values are given in days. Hu et al. (2012) reported periodicity values in three of the fossil orangutan Chinese apothecary teeth included here, which are in agreement with the current study.

^a Living *Pongo* values represent the average of all wild and captive individuals.

greater than living orangutans (3.94 microns/day), a trend towards significance ($p = 0.051$).

The long-period line periodicity ranged between 9 and 10 days in 12 living orangutans, with minor differences between species, and an overall mean of 9.5 days (Table 5). Comparisons of known sex individuals revealed a non-significant trend ($Z = -1.556$, $p = 0.120$) for females to show greater values than males (females = 9.8 days, $n = 5$; males = 9.2 days, $n = 4$). The long-period line periodicity in 15 of the 20 fossil individuals ranged from 9 to 12 days, with an average of 10.1 days. In five fossil individuals, it was not possible to determine a precise value; estimates ranged from 8 to 13 days. Comparisons of long-period line periodicity values revealed that the fossil sample was not significantly different from the living orangutan sample ($Z = -1.576$, $p = 0.152$).

Visual inspection of cusp-specific crown formation times revealed that neither sex showed consistently greater values within each living orangutan species (Appendix), thus males and females were lumped for subsequent analyses. Sumatran orangutans showed slightly longer crown formation times than Bornean orangutans in six of eight possible comparisons; values were lumped for further comparisons because of limited sample sizes. Crown formation times in living orangutans ranged from 764 to 1794 days depending on tooth type and molar position (Table 6); a maxillary second molar mesiolingual cusp was excluded as it was not clear if formation was complete at 1806 days. The lingual cusps of maxillary molars typically showed longer formation times than respective buccal cusps within the mesial or distal plane, whereas

the opposite pattern was consistently found in mandibular molars. Crown formation times varied within cusp types among molars positions, generally increasing from M1 to M2. Because of uncertainty in the serial molar position of the isolated fossil teeth, comparisons of cusp-specific crown formation times and extension rates were made to the combined sample of living orangutan M1–M3s. Crown formation times in fossil orangutan molars were greater than in living orangutans, exceeding living values in four of six comparisons (Table 6, Fig. 2). Extension rates tended to be greater in living orangutans than in fossil orangutans; mean values in the fossil sample fell below living orangutan ranges in two of six comparisons (Table 7). Sample sizes were too small to permit statistical comparisons of crown formation times or extension rates among cusps or molars, or between sexes, species, or living and fossil orangutans.

The average prenatal DSR in living orangutans is 3.02 microns/day ($n = 11$ cusps, standard deviation = 0.49 microns/day). First molar initiation ages range from 75 days before birth (mandibular M1 mesiobuccal cusp) to 12 days after birth (maxillary M1 distolingual cusp), with mesiobuccal and distobuccal cusps initiating approximately one month before birth on average (Table 8). Data from several other cusps were omitted as it was not possible to be confident about the identification of neonatal lines or the precise timing of initiation. The age at completion was determined in ten M1 cusps of known initiation ages, which ranged from 992 days (maxillary M1 mesiolingual cusp) to 1756 days of age (mandibular M1 mesiobuccal cusp; Table 8).

One wild-shot Bornean individual (MCZ 5290) was estimated to have died at 4.5 years of age (1646–1657 days). By this age the maxillary and mandibular M1s were in full occlusion (Fig. 3) and the rest of the permanent dentition had yet to near eruption or complete crown calcification (Fig. 4). A second Bornean individual (ZSM 1981/48) was estimated to be ~8.4 years of age when it was shot; the uncertainty associated with this age is approximately ± 1 month as a consequence of matching broad elemental bands in dentine with accentuated lines in enamel. The maxillary and mandibular M1s and M2s were emergent, while the rest of the permanent dentition had yet to erupt. Protein stains covered the M2 crowns but attrition was very minor. First and second molar crown formation overlapped by a minimum of one year (maxillary

Table 6
Molar crown formation times (in days) for living and fossil orangutans.

Taxon	Tooth	mb	Range (n)	ml	Range (n)	db	Range (n)	dl	Range (n)
Living <i>Pongo</i>	UM1	1064	1006–1144 (4)	1119	1028–1210 (2)	1044	– (1)	1170	1086–1254 (2)
	UM2	1203	1058–1405 (3)	1289	1213–1336 (3)	1374	1203–1544 (2)	1457	– (1)
	UM3	1133	1064–1202 (2)	1092	– (1)	1698	– (1)	n/a	n/a
	LM1	1373	1082–1794 (5)	858	807–910 (2)	1271	1026–1489 (3)	882	764–986 (3)
	LM2	1330	1272–1394 (3)	1036	1003–1069 (2)	n/a	n/a	1115	833–1427 (5)
	LM3	1469	– (1)	1074	1051–1098 (2)	1342	– (1)	1004	900–1141 (4)
Fossil <i>Pongo</i> ^a	UM	1583	– (1)	1978	– (1)	n/a	n/a	1950	– (1)
	LM	1550	– (1)	1340	1150–1466 (3)	n/a	n/a	1158	– (1)

Tooth: U = upper/maxillary, L = lower/mandibular, M = molar. Cusps: mb = mesiobuccal, ml = mesiolingual, db = distobuccal, dl = distolingual. Average values are given in days for each cusp, followed by the range and sample size.

^a These four isolated fossil teeth from China cannot be assigned to specific molar positions with absolute certainty.

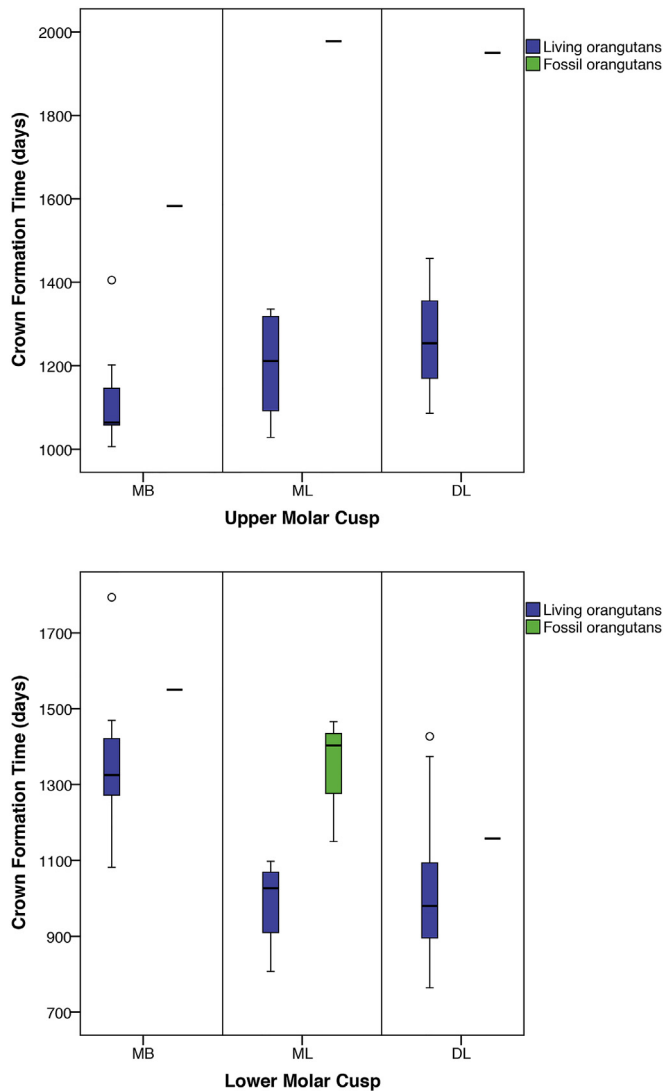


Figure 2. Cusp-specific crown formation times in living and fossil orangutan molars. Molars (M1–M3) were combined as there is some uncertainty in the serial position of the four fossil molars included here. Cusp types are as follows: MB = mesiobuccal, ML = mesiolingual, DL = distolingual. Standard box and whisker plot reveals the interquartile range (25th–75th percentiles: boxes), 1.5 interquartile ranges (whiskers), and the median values (black line). Outliers more than 1.5 interquartile ranges from the box are signified with circles.

M1 distolingual cusp completion: 1266 days of age, mandibular M2 mesiobuccal cusp initiation: ~900 days of age). The M2 and M3 crowns overlapped by a minimum of four months (mandibular M2 mesiobuccal cusp completion: ~2294 days of age, LM3 mesiolingual cusp initiation: ~2172 days of age). Minimum ages are given as it was not possible to ensure that the earliest- and latest-forming cusps were compared in each successive molar pair. Maxillary M3s initiated later than mandibular M3s; the maxillary distolingual cusp initiated ~5–7 months after the mandibular distolingual and mesiolingual cusps, respectively. Neither maxillary or mandibular M3s had completed crown formation prior to death at ~8.4 years of age.

The age at death for wild-shot Sumatran individual ZMB 83508 was estimated at 8.8 years (~3229 days). By this age, the following permanent teeth had completely erupted: maxillary first molars, mandibular central and lateral incisors, fourth premolars, and first and second molars (Fig. 5). The following teeth were almost completely emergent when the individual died: maxillary central incisors, third premolar (right side only), second molars, and mandibular third premolars. The maxillary lateral incisors had emerged past the alveolar margin but did not show any protein stains, thus it is unlikely that these teeth had pierced the gingiva prior to death. This individual retained its deciduous maxillary canines and fourth premolars. The timing of molar cusp initiation and completion are given in Figure 1 for ZMB 83508. The degree of developmental overlap between successive molars was also estimated; M1 and M2 crowns overlapped by a minimum of 169 days, while M2 and M3 overlapped by a minimum of 364 days.

A second wild Sumatran individual (ZSM 1981/246) was estimated to be ~8.5 years of age (~3089 days) when it was shot. The maxillary and mandibular M1s were fully occluded with light wear, but the rest of the permanent dentition had yet to erupt. This male individual had very large molar crowns and extreme pathology, including molar crowding, multiple hypoplasias, and possible ‘dens in dente’ in the right maxillary M3 (Reid, pers. comm.). During tooth removal it became apparent that the mandibular M3s were developing superior and/or anterior to the M2s (Fig. 6), which were likely to have been impacted. The mandibular M1 mesiobuccal cusp was complete at 4.8 years of age, thus molar eruption was unlikely to have occurred prior to ~6 years of age. First and second molar crown formation overlapped by a minimum of 473 days (mandibular M1 mesiobuccal cusp completion: 1756 days of age, maxillary M2 mesiolingual cusp initiation: ~1283 days of age). The right mandibular M3 mesiobuccal cusp had been forming for approximately 560 days prior to death, which largely overlapped the formation of the maxillary M2 mesiolingual cusp that was near completion when the individual died at approximately 3089 days of age. The maxillary M3s were not extracted from this individual.

Table 7

Molar extension rates (in microns/days) for living and fossil orangutans.

Taxon	Tooth	mb	Range (n)	ml	Range (n)	db	Range (n)	dl	Range (n)
Living <i>Pongo</i>	UM1	6.12	5.46–6.98 (4)	6.42	6.23–6.61 (2)	7.46	– (1)	6.03	5.68–6.38 (2)
	UM2	5.83	4.78–7.60 (3)	5.28	4.59–5.86 (3)	4.71	4.65–4.77 (2)	4.58	– (1)
	UM3	4.46	4.22–4.69 (2)	5.56	– (1)	4.86	– (1)	n/a	n/a
	LM1	5.98	4.55–7.08 (5)	7.21	7.14–7.28 (2)	5.96	5.49–6.81 (3)	5.38	4.61–5.94 (3)
	LM2	5.61	4.93–6.00 (3)	5.17	5.00–5.33 (2)	n/a	n/a	4.62	4.40–4.88 (5)
	LM3	4.83	– (1)	5.41	5.31–5.50 (2)	4.80	– (1)	4.30	3.59–5.02 (4)
Fossil <i>Pongo</i> ^a	UM	4.92	– (1)	4.50	– (1)	n/a	n/a	3.91	– (1)
	LM	5.14	– (1)	5.17	4.46–5.80 (3)	n/a	n/a	4.54	– (1)

Tooth: U = upper/maxillary, L = lower/mandibular, M = molar. Cusps: mb = mesiobuccal, ml = mesiolingual, db = distobuccal, dl = distolingual. Average values are given in microns/day for each cusp, followed by the range and sample size.

^a These four isolated fossil teeth cannot be assigned to specific molar positions with absolute certainty.

Table 8

First molar cusp initiation ages (in days before birth), crown formation times (in days), and completion ages (in days) in living orangutans.

Taxon	Individual	Tooth	mb	CFT	Age	ml	CFT	Age	db	CFT	Age	dl	CFT	Age
<i>Pongo pygmaeus</i>	ZSM 1981/48	RUM1	–29	–	–	5	–	–	–	1044	–	12	1254	1266
	" "	LUM1	–5	1144	1139	10	1210	1220	–40	–	–	–	–	–
	ZSM 1981/87	LUM1	–	–	–	–	–	–	–	–	–	–	1086	–
	MCZ 5290	RUM1	–	1060	–	–36	1028	992	–	–	–	–	–	–
	ZD.1976.1444	RUM1	–	1006	–	–	–	–	–	–	–	–	–	–
	ZSM 1981/48	LLM1	–	1304	–	–	–	–	–	1297	–	–	–	–
	ZSM 1981/87	LLM1	–	–	–	–	807	–	–	–	–	–	764	–
	ZD.1976.1439	RLM1	–43	1265	1222	–	–	–	–	–	–	–	986	–
	ZD.1976.1444	LLM1	–	–	–	–	–	–	–	–	–	–	896	–
	MCZ 5290	LLM1	–75	1082	1007	–	910	–	–	–	–	–	–	–
	ZSM 1981/246	LUM1	–34	–	–	–	–	–	–	–	–	–	–	–
	ZSM 1981/248	LUM1	–	–	–	–	–	–	–8	–	–	–	–	–
<i>Pongo abelii</i>	ZMB 83508	RUM1	–40	1046	1006	–	–	–	–	–	–	–	–	–
	ZSM 1981/246	RLM1	–34	–	–	–	–	–	–	–	–	–	–	–
	" "	LLM1	–38	1794	1756	–	–	–	–	–	–	–	–	–
	ZMB 83508	RLM1	–	–	–	–	–	–	–29	1026	997	–	–	–
	HT 162/166	LLM1	–23	1421	1398	–21	–	–	–	1489	–	–	–	–

Tooth: R = right, L = left; U = upper/maxillary, L = lower/mandibular, M = molar. Initiation ages are given for each cusp in days relative to birth. Cusps: mb = mesiobuccal, ml = mesiolingual, db = distobuccal, dl = distolingual. Crown formation times (CFT) are given for each respective cusp in days. Completion ages (Age) are given for each respective cusp in days after birth.

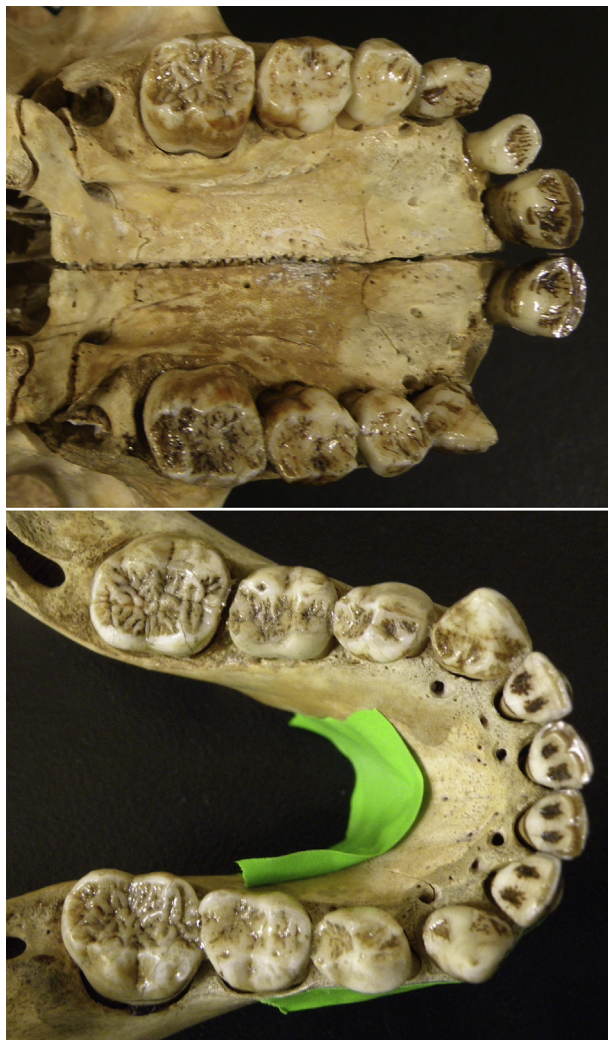


Figure 3. Eruption status of the permanent dentition of a 4.5 year-old wild-shot Bornean orangutan juvenile (MCZ 5290). The maxillary dentition is above, mandibular dentition below. Images are not to the same scale. Note the extensive brown protein stains and light wear on the M1s, demonstrating that these teeth had been emergent for some time prior to death. Tape was used to hold the mandible together as it had fractured across the canine crypt. Specimen courtesy of the Museum of Comparative Zoology, Harvard University.

4. Discussion

4.1. Incremental development in living orangutans

This study confirms the trend noted by [Beynon et al. \(1998\)](#) and others that orangutan daily secretion rate (DSR) values increase markedly from inner to middle cuspal regions, and less dramatically from middle to outer cuspal regions. [Beynon et al. \(1991b\)](#) presented cuspal DSR measurements from four captive orangutan molar sections (inner: 3.3 microns/day, middle: 4.7 microns/day, outer: 5.3 microns/day), which are slightly greater than the values in the current study. [Smith \(2008\)](#) suggested that methodological differences can impact DSR comparisons, as Beynon, Dean, and Reid typically measure DSR in the middle and outer enamel lateral to the cuspal axis to avoid excessive prism decussation, which are areas of thicker enamel and higher DSRs than the cuspal midline. In the current study, a significant negative correlation was found between the daily secretion rate and the visually estimated correction factor (Pearson's $r = -0.602$, $p < 0.001$, $n = 53$). Thus molar cusps with more gnarled or decussated enamel showed lower overall DSR values than those with straighter enamel prisms from the dentine horn to the cusp tip.

Long-period line periodicity values for living orangutans in the current study are similar to earlier reports ([Beynon et al., 1991a](#); [Schwartz et al., 2001](#); [Kelley and Schwartz, 2010](#)), although the range for the 12 individuals (9–10 days) is narrower than values reported by [Schwartz et al. \(2001: 8–11 days\)](#) and [Kelley and Schwartz \(2010: 9 and 11 days\)](#). The value of 10 days was confirmed for the individual studied by [Beynon et al. \(1991a\)](#). It is clear that large samples are needed to capture periodicity values at the tails of distributions, as is the case for living humans (6–12 days: [FitzGerald, 1995](#); [Reid and Dean, 2000](#); [Schwartz et al., 2001](#); [Smith et al., 2007c](#)) and chimpanzees (5–9 days: [Schwartz et al., 2001](#); [Smith et al., 2007b, 2010a](#); [Kierdorf et al., 2015](#)).

[Beynon et al. \(1991a\)](#) undertook the first comprehensive histological study of orangutan dental development in a captive male individual of unknown geographic origin, and the molars of this individual were reanalyzed during the current study. Data on molar crown formation times were not presented for specific cusps in the original study, limiting comparisons with the new data, although [Beynon et al. \(1991a\)](#) noted that times differed by as much as 20% among cusps. The crown formation time of the maxillary M1 was reported to be 2.74 years, which is presumably from the

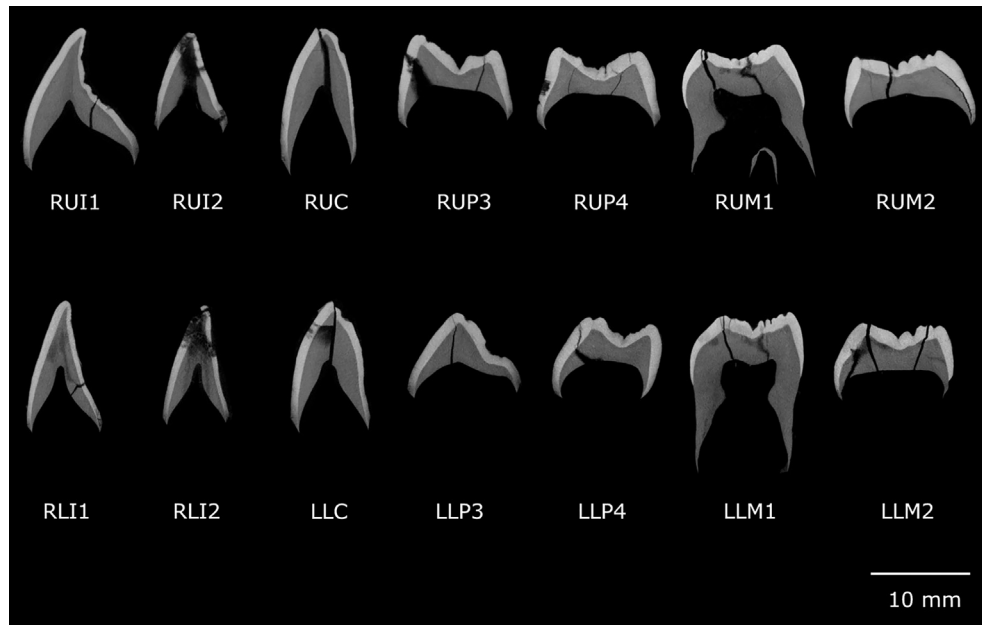


Figure 4. Calcification status of the permanent dentition of a 4.5 year-old Bornean orangutan juvenile (MCZ 5290) revealed by micro-CT imaging. Tooth types are as follows: R = right, L = left, U = upper/maxillary, L = lower/mandibular, I = incisor, C = canine, P = premolar, M = molar. Micro-CT scans did not reveal any M3 crowns or cusps, although large crypts were present in the mandible.

mesiolingual cusp, as the mesiobuccal cuspal enamel had been worn away. Reanalysis suggests that this was likely underestimated by several months, as wear resulted in a substantial loss of cuspal enamel and long-period lines (prohibiting inclusion in the current study.) New crown formation times determined for the six well-preserved molar cusps from this individual are as follows: LM1 mesiobuccal cusp 3.89 years, LM1 distobuccal cusp 4.08 years, UM2 distobuccal cusp 4.23 years, LM2 distolingual cusp 3.76 years, LM3 distolingual cusp 3.13 years, and UM3 distobuccal cusp 4.65 years. These times are similar to values independently determined by Don Reid subsequent to the [Beynon et al. \(1991\)](#) report using current analytical methods (Reid, pers. comm.). In summary, the duration of molar formation is approximately one year greater for each molar of this individual than the times depicted in [Beynon et al. \(1991a: Fig. 8, p. 200\)](#).

This study provides new ages for orangutan molar initiation; M1s of Bornean and Sumatran orangutans begin forming approximately one month before birth, with some variation among cusps. These results are consistent with [Winkler et al. \(1991\)](#), who dissected a stillborn captive orangutan and reported that three cusps on each M1 had begun calcification before birth. [Oka and Kraus \(1969\)](#) and [Winkler \(1995\)](#) report that a fourth molar cusp also began calcification prior to birth in other perinatal orangutans. Three wild individuals in the current study showed M2 initiation ages between 2.3 and ~3.5 years of age, which varies between maxillary and mandibular analogues as well as among cusps, and complicates comparisons with published data. [Winkler et al. \(1991\)](#) confirmed the presence of well-developed unspecified M2 cusps in a dissection of a 17-month old captive individual, and later reported M2 calcification had also commenced in a deceased 16-month old captive individual ([Winkler, 1995](#)). In their innovative study of a captive orangutan juvenile, [Beynon et al. \(1991a\)](#) presented a chronology of dental development based on the presence of tetracycline lines ([Beynon et al., 1991a: Figs. 8 and 9, p. 200](#)), which serve as externally induced markers in teeth forming at the same time. They reported that M2 initiation occurred at approximately two years of age, and that M3 initiation occurred after 4.5 years of age. Given the likelihood that M1 crown formation time was

underestimated in their study, it follows that the timing of the first tetracycline line (TCL 1: 2.0 years) used to register other developing teeth and determine initiation ages of the rest of the dentition was also underestimated. Third molar initiation in the three wild individuals in the current study ranged from 5.2 to ~6.9 years; precise comparative data on M3 initiation are not currently available.

This study also provides important information on tooth eruption from wild orangutan juveniles whose ages were histologically determined. The 4.5 year-old Bornean individual died with fully erupted maxillary and mandibular M1s, and their emergence must have occurred prior to [Kelley and Schwartz's \(2010\)](#) estimates from two wild-shot Bornean juveniles (4.5–4.6 years). Little is known about M1 emergence in Sumatran orangutans. Gustav Brandes carefully studied a captive male of Sumatran descent named “Buschi” for more than a decade. [Brandes \(1939\)](#) first stated that the M1 emerged at 3.5 years (without specifying the maxillary or mandibular position), and then illustrated maxillary M1 eruption in a schematic, stating in the caption “M1 from 4 years” ([Brandes, 1939: Fig. 122, p. 88](#)). As [Smith et al. \(1994\)](#) notes, these ages may be somewhat imprecise as [Brandes \(1939\)](#) appeared to round all ages to the half year. In another early report of dental development, [Schultz \(1941\)](#) states that a female of unspecified geographic origin from the Philadelphia Zoo had yet to erupt her M1s at three years and three months of age.

Data on age at M1 crown completion ([Table 8](#)) are relevant to this discussion as molar eruption occurs substantially later than crown completion; one wild Sumatran male and one captive male showed M1 crown completion ages later than 4 years of age. [Kelley and Schwartz \(2010\)](#) estimated that the time between M1 crown completion and molar eruption in two wild orangutans was slightly less than 1.5 and 1.8 years. Studies of chimpanzee development also suggest that eruption occurs ~1–2 years after crown formation is complete (reviewed in [Smith et al., 2007b; Dean and Kelley, 2012](#)). While additional data are needed to provide precise estimates of eruption from the age of crown formation, it is likely that M1 eruption ages may exceed 5 and possibly 6 years in some orangutans.

Second molar emergence in the 8.8 year-old Sumatran individual in the current study likely occurred later than in Buschi;



Figure 5. Eruption status of the permanent dentition of an 8.8 year-old wild shot Sumatran orangutan juvenile (ZMB 83508). The maxillary dentition is above, mandibular dentition below. Images are not to the same scale. Note the angled protein stains and light wear on the M2s.

Fooden and Izor (1983) and Smith et al. (1994) reported that his M2s emerged at 5 years of age. However, Brandes' (1939) study, which is in German, states that the M2s emerged towards the end of the fifth year (p. 88), and the caption of the schematic discussed above states "M2 from 6 years." Data on the emergence of Buschi's other teeth are less precise, and their ages are reported by Brandes (1939) as wide intervals (summarized in Fooden and Izor, 1983; Smith et al., 1994). Data from the ~8.4 and 8.8 year-old individuals suggests that M3 eruption would not have occurred for several more years as the M3 crowns had yet to complete formation. Unfortunately, it was not possible to assign ages to the orangutans in this study that had erupted their M3s, thus no data currently exist for M3 eruption age in wild orangutans. Additional individuals are needed to determine if there are consistent differences in molar development between captive and wild individuals, orangutan species, or sexes beyond those sex differences documented for canine formation (Schwartz and Dean, 2001; Schwartz et al., 2001).

4.2. Dental development in living great apes and humans

Numerous studies have characterized incremental dental development in great apes and humans (reviewed in Dean, 2000;



Figure 6. Molar crowding in a ~8.5 year-old male Sumatran orangutan (ZSM 1981/246). The upper panel shows the left mandibular molar row after removal of part of the ramus and alveolar bone; from left to right: M3, M2, M1 erupted. The lower panel displays the right mandibular molar row; from left to right: M1 erupted, M3, M2. The left mandibular M3 crown was nearly 20 mm long, while the right mandibular M3 cusps were formed in atypical positions, and enamel was observed within the coronal dentine on the undersurface of the developing crown (possible dens in dente.).

Smith, 2008). Linear measures of enamel thickness in orangutan molar cusps are approximately two times thicker than chimpanzees and are more similar to modern humans (Smith et al., 2007b, 2010a; also see scaled values in Schwartz, 2000). This is relevant for understanding patterns of dental development as great ape and human average DSR values (Table 9) do not differ significantly ($\chi^2 = 6.679$, $p = 0.083$), suggesting that differences in enamel thickness contribute to variation in crown and/or cuspal formation times (discussed further below).

Orangutans show the highest long-period line periodicity values of any living primate ($x = 9.5$ days), including humans (reviewed in Smith, 2008: Table 2, p. 213; Bromage et al., 2009: Table 1, pp. 390–391). Long-period line periodicity is known to show a significant positive correlation with body mass broadly across primates

Table 9
Daily secretion rate (in microns/day) in the cuspal enamel of living great ape and human molars.

Taxon	n	Inner	Middle	Outer	Mean
Gorilla	9	3.10	4.14	4.70	3.98
Homo	21	2.55	4.34	5.45	4.11
Pan	86	3.58	4.20	4.55	4.08
Pongo	53	3.23	4.08	4.52	3.94

All values are given in microns/day. Gorilla data are unpublished data from Green et al. (2011), while Homo and Pan values derive from Smith et al. (2007b, c, 2010a) and unpublished data.

(Smith, 2008; Bromage et al., 2009), although this relationship does not hold in interspecific comparisons among great apes, nor when similarly sized female chimpanzees and orangutans are compared. Periodicity values in 10 chimpanzee females averaged 6.9 days, while 12 orangutan females averaged 9.4 days (Schwartz et al., 2001). These authors also found a trend for orangutan females to show higher mean periodicity values than males, as in the current study, although this was not significant. Smith et al. (2007c) report that human females from South Africa showed significantly higher periodicity values than South African males. Larger and more diverse samples are needed to determine if sex differences in periodicity values are apparent in other non-human primates or human populations, and to understand how factors other than body mass relate to long-period line periodicities in great apes and humans.

Molar formation times, crown formation times, and M1 eruption ages vary within and among great ape genera (e.g., Beynon et al., 1991a; Schwartz et al., 2006; Smith et al., 2007b, 2013; Kelley and Schwartz, 2010; Machanda et al., 2015). Average crown formation times in great apes and human molar cusps range from 1.73 to 4.65 years, with substantial variation among cusps (Table 10). Chimpanzees tend to show the shortest crown formation times, in contrast to the prolonged times of orangutans. Limited data on gorillas tentatively place them in an intermediate position, but more data are required to determine how they compare to other hominoids, as sample sizes are quite small. Modern human crown formation times exceed those of chimpanzees and are more similar to gorillas and orangutans, depending on the molar and cusp being compared.

The long formation times documented here for the captive orangutan studied by Beynon et al. (1991a) may be surprising, as some have suggested that dental development is more rapid in captivity than in the wild (reviewed in Kelley and Schwartz, 2010; Smith et al., 2010a). New values for this individual are generally greater than values for wild-shot individuals and a second captive

individual in the current study, as well as the two M1s from wild Bornean individuals reported by Kelley and Schwartz (2010). Crown formation times in chimpanzee and gorilla molars also show considerable overlap between captive and wild individuals (Beynon et al., 1991a; Schwartz et al., 2006; Smith et al., 2007b, 2010a; Kelley and Schwartz, 2010), thus captivity does not appear to have a consistent effect in accelerating crown formation.

Formation time may relate to absolute tooth size, although gorillas have the largest molars among the living hominoids and do not show the longest formation times. Smith (2004) proposed quantifying the cusp-specific extension rate as a means to standardize development time across teeth that differ in size. This metric reveals fairly consistent taxonomic differences among great apes and humans (Table 11); gorillas form their large molar crowns more rapidly than chimpanzees and orangutans, while humans and orangutans show the slowest extension rates (which were even slower in fossil orangutans). The pattern of coronal extension rate variation appears to be consistent with differences in the rate of molar root extension among great apes (Beynon et al., 1991a; Smith et al., 2007b). A comparison of Tables 9 and 11 illustrates that extension rates are more variable among great apes and humans than daily secretion rate. Enamel-forming cells may be constrained to secrete enamel at a fairly constant daily rate, while the speed of their activation (or total number of cells secreting enamel) is more plastic.

Long molar crown formation times necessitate late eruption ages, particularly for first molars, which consistently initiate about a month before birth. Orangutans typically complete deciduous tooth eruption by one year of age (Lippert, 1977; Fooden and Izor, 1983), which is earlier than chimpanzees and humans (reviewed in Machanda et al., 2015), but they have been reported to show later M1 eruption ages than other great apes (Brandes, 1939; Kelley and Schwartz, 2010). However, novel data on M1 eruption from a 4.5 year-old wild Bornean orangutan coupled with the absence of M1s in two similarly-aged wild chimpanzees (Kelley et al., 2014) implies a higher degree of developmental overlap among great apes than

Table 10

Average molar crown formation times (in days and years) in living great apes and humans.

Tooth	Taxon	CFT (days)				CFT (years)			
		mb	ml	db	dl	mb	ml	db	dl
UM1	<i>Gorilla</i>	784	994	n/a	1168	2.15	2.72	n/a	3.20
	<i>Homo</i>	1065	1172	n/a	1143	2.92	3.21	n/a	3.13
	<i>Pan</i>	867	775	852	684	2.38	2.12	2.33	1.87
	<i>Pongo</i>	1064	1119	1044	1170	2.92	3.07	2.86	3.21
UM2	<i>Gorilla</i>	1032	1057	1285	1136	2.83	2.90	3.52	3.11
	<i>Homo</i>	1132	1230	1175	1131	3.10	3.37	3.22	3.10
	<i>Pan</i>	1084	1013	1511	n/a	2.97	2.77	4.14	n/a
	<i>Pongo</i>	1203	1289	1374	1457	3.30	3.53	3.76	3.99
UM3	<i>Gorilla</i>	n/a	1554	n/a	1468	n/a	4.26	n/a	4.02
	<i>Homo</i>	1165	1234	n/a	n/a	3.19	3.38	n/a	n/a
	<i>Pan</i>	921	1035	821	926	2.52	2.84	2.25	2.54
	<i>Pongo</i>	1133	1092	1698	n/a	3.10	2.99	4.65	n/a
LM1	<i>Gorilla</i>	933	888	1143	845	2.55	2.43	3.13	2.31
	<i>Homo</i>	1140	986	1125	983	3.12	2.70	3.08	2.69
	<i>Pan</i>	797	633	811	662	2.18	1.73	2.22	1.81
	<i>Pongo</i>	1373	858	1271	882	3.76	2.35	3.45	2.42
LM2	<i>Gorilla</i>	1241	965	1118	947	3.40	2.64	3.06	2.59
	<i>Homo</i>	1164	983	n/a	n/a	3.19	2.69	n/a	n/a
	<i>Pan</i>	1009	847	1160	842	2.76	2.32	3.18	2.31
	<i>Pongo</i>	1330	1036	n/a	1115	3.64	2.84	n/a	3.05
LM3	<i>Gorilla</i>	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	<i>Homo</i>	1181	1038	1244	1213	3.24	2.84	3.41	3.32
	<i>Pan</i>	1001	823	1120	821	2.74	2.25	3.07	2.25
	<i>Pongo</i>	1469	1074	1342	1004	4.02	2.94	3.68	2.75

Tooth: U = upper/maxillary, L = lower/mandibular, M = molar. Cusps: mb = mesiobuccal, ml = mesiolingual, db = distobuccal, dl = distolingual. *Gorilla* data are from Green et al. (2011), while *Homo* and *Pan* values derive from Smith et al. (2007b, c, 2010a, b).

Table 11

Molar crown extension rates (in microns/day) in living great apes and humans.

Tooth	Taxon	mb	ml	db	dl
UM1	<i>Gorilla</i>	10.05	11.12	n/a	8.34
	<i>Homo</i>	5.87	5.82	n/a	5.53
	<i>Pan</i>	7.17	7.86	8.00	7.27
	<i>Pongo</i>	6.12	6.42	7.46	6.03
UM2	<i>Gorilla</i>	8.87	9.53	8.65	9.49
	<i>Homo</i>	5.80	5.34	6.22	4.93
	<i>Pan</i>	5.19	6.11	4.58	n/a
	<i>Pongo</i>	5.83	5.28	4.71	4.58
UM3	<i>Gorilla</i>	n/a	5.89	n/a	5.71
	<i>Homo</i>	5.32	5.31	n/a	n/a
	<i>Pan</i>	5.91	5.48	5.80	4.99
	<i>Pongo</i>	4.46	5.56	4.86	n/a
LM1	<i>Gorilla</i>	11.28	9.75	9.25	8.71
	<i>Homo</i>	6.61	6.30	5.90	6.11
	<i>Pan</i>	7.94	8.82	8.08	7.88
	<i>Pongo</i>	5.98	7.21	5.96	5.38
LM2	<i>Gorilla</i>	9.22	7.82	7.32	7.20
	<i>Homo</i>	5.68	5.73	n/a	n/a
	<i>Pan</i>	6.37	6.59	5.91	6.33
	<i>Pongo</i>	5.61	5.17	n/a	4.62
LM3	<i>Gorilla</i>	n/a	n/a	n/a	n/a
	<i>Homo</i>	5.64	5.49	n/a	n/a
	<i>Pan</i>	7.23	6.60	5.10	6.22
	<i>Pongo</i>	4.83	5.41	4.80	4.30

Tooth: U = upper/maxillary, L = lower/mandibular, M = molar. Cusps: mb = mesiobuccal, ml = mesiolingual, db = distobuccal, dl = distolingual. All values are given in microns/day. *Gorilla* data are from Green et al. (2011), while *Homo* and *Pan* data are from Smith et al. (2007b, 2010a, b).

previously recognized. While M1 emergence age has been employed as a classic skeletal benchmark of primate life history scheduling (e.g., Smith, 1989; Smith et al., 1994; Dean et al., 2001; Kelley and Schwartz, 2010, 2012), recent work has pointed out limitations of this theory among closely related taxa such as great apes and humans (e.g., Robson and Wood, 2008; Humphrey, 2010; Smith et al., 2013; reviewed in Smith, 2013). Long-term studies of molar eruption and life history within wild primates (e.g., Machanda et al., 2015) and traditional human societies may provide much needed clarification of the strength of association and predictive power of dental development for hominoid life history reconstruction.

It is now possible to refine several of the assumptions of Dean and Wood (1981)'s landmark radiographic study of great ape tooth development. Great ape M1s initiate approximately one to two months before birth, followed by M2s that typically initiate prior to the completion of M1s (leading to developmental overlap in crown calcification; Beynon et al., 1991a; Winkler et al., 1991; Winkler, 1995; Anemone et al., 1996; Schwartz et al., 2006; Smith et al., 2007b). Great ape molars require ~2–5 years to complete their formation, which varies among molar positions, cusps, and taxa. Much less is known about the rate and duration of root formation or posterior molar emergence ages, although the data reviewed above suggest that developmental variation is likely to complicate the detection of subtle differences in small samples. For example, the calcification status of a 4.5 year-old Bornean orangutan juvenile's dentition (Fig. 4) appears to be advanced in comparison to a 4.4 year-old Liberian chimpanzee (Fig. 7). Calcification standards from known-age great apes (e.g., Anemone et al., 1996; Kuykendall, 1996; Winkler et al., 1996; Smith et al., 2010a) must be expanded in order to produce accurate chronologies and to determine the degree of similarities and differences. While it is clear that modern humans show a prolonged period of dental development compared to great apes, as Dean and Wood (1981) highlight, intriguing similarities between living orangutans and humans warrant further investigation.

4.3. Paleobiological implications

This is the first study to assess molar crown formation in congeneric living and fossil great apes, which may complement our understanding of developmental variation in the genus *Homo*. Although Smith et al. (2011) found that fossil orangutans have greater average enamel thickness values than living orangutans (calculated as the area of the enamel cap divided by the enamel–dentine junction length), similar trends in linear measurements of cuspal enamel thickness were not found to be significant in the current study. Enamel thickness is highly variable, and is it likely that significant differences would emerge in larger samples,

particularly in comparisons of M1s. However, slight differences in cuspal enamel thickness values are unlikely to explain longer formation times, as fossil orangutans also show higher cuspal daily section rates, and cuspal formation time is the quotient of enamel thickness divided by DSR. This sample of fossil and living orangutans shows nearly equivalent long-period line periodicity values (also see Hu et al., 2012), but differences in long-period line numbers. The fossil molars have higher numbers of long-period lines, which results in longer crown formation times than living orangutans (as are they are multiplied by the long-period line periodicity to determine the lateral formation time). These differences are reflected in lower extension rates in fossil orangutans. In summary, the smaller molars of living orangutans have a shorter period of lateral enamel formation characterized by fewer long-period lines and a faster rate of extension (cell addition) than fossil orangutans. This appears to be similar to the pattern found in living humans when compared to an early *Homo sapiens* individual from northern Africa (Smith et al., 2007a).

Fossil *Homo* species demonstrate considerable variation in molar formation, ranging from short molar formation times in *Homo erectus* (Dean et al., 2001) and *Homo neanderthalensis* (Smith et al., 2009, 2010b), to modern human-like values in an early *Homo* individual from Drimolen, South Africa (Smith et al., 2015), and extremely long times in the early *H. sapiens* individual from northern Africa (Smith et al., 2007a). This latter case was ascribed to absolute differences in tooth size; *H. sapiens* and *Pongo* share a parallel trend of dental reduction during the Pleistocene. Smith et al. (2011) proposed that this reduction was achieved through different trends in each taxon; orangutans show nearly equal losses in the enamel and dentine making up the tooth crown, while humans appear to have preferentially reduced the coronal dentine more than the enamel component.

Changes in tooth size and tissue volumes may result from differences in the developmental mechanisms of molar crown formation. Grine and Martin (1988) postulated that the amount of enamel on a tooth crown is the result of several variables: 1) DSR, 2) duration of secretion (crown formation time), and/or 3) number of active secretory cells. Comparisons of DSRs suggest that early *Homo* groups (excluding *H. erectus*) show more rapid values than living humans, while cuspal DSR in *H. erectus* and Neanderthals appears to be relatively similar to living humans, as is the case for a *H. sapiens* individual from Skhul (Dean et al., 2001; Dean, 2007; Lacruz et al., 2008; Smith et al., 2009, 2015). Fossil orangutans appear to show slightly greater DSR values than living orangutans ($p = 0.051$), representing another potential convergence with early members of the genus *Homo*. As noted above, crown formation time varies markedly across fossil *Homo* species, with the longest times found in an early *H. sapiens* individual (Smith et al., 2007a). Similarly prolonged molar formation times are apparent in fossil

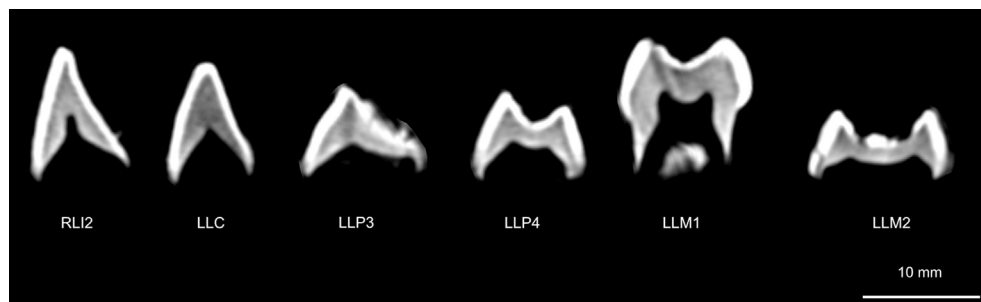


Figure 7. Calcification status of a 4.4 year-old wild chimpanzee mandibular dentition. The permanent teeth of this individual had not erupted prior to death at 4.4 years of age, although the mesial M1 cusps had surpassed the alveolar margin (Kelley and Schwartz, 2012; Kelley et al., 2014). This figure is included for qualitative assessment only as the spatial resolution of this CT scan is markedly lower than the individual in Figure 4.

orangutans, particularly in the associated maxillary and mandibular molar crowns from Ganqian Cave (China), which exceed current living orangutan ranges. Grine and Martin's (1988) final determinate of molar enamel is the number of active secretory cells, which can be approximated by the long-period lines that delineate the former active secretory front. Another proxy for this variable is the extension rate, or the length of the enamel–dentine junction divided by the total time of formation. Relatively little is known about coronal extension rates in fossil *Homo*. Smith et al. (2010b) demonstrated that living and fossil *H. sapiens* generally show slower extension rates than Neanderthals. The large crowns of fossil orangutans, like the early *H. sapiens* individual, are the result of particularly long formation times/slow extension rates that fall outside of the ranges of their modern analogues for certain cusps.

Finally, data on molar crown formation in living and fossil orangutans is relevant for studies of Miocene hominoid dental development, particularly in taxa that have been postulated to be ancestral to orangutans such as *Sivapithecus* and *Lufengpithecus*. Living and fossil orangutans show slower DSRs and longer crown formation times than *Sivapithecus* species (Mahoney et al., 2007), although reported long-period line periodicities overlap (8–9 days, $n = 2$). Similarly, both living and fossil *Pongo* have slower DSRs and higher long-period line periodicities than *Lufengpithecus* species (Schwartz et al., 2003). These authors note that one *Lufengpithecus hudienensis* M1 from Yuanmou shows a short crown formation time, while preliminary data on two *Lufengpithecus lufengensis* M2s are very similar to living orangutans and exceed times reported for any other Miocene hominoids. Orangutans show some similarities with *Gigantopithecus blacki*, which was contemporaneous with fossil *Pongo*, and has a long-period line periodicity of 11 days ($n = 1$) and M3 cusp-specific crown formation times that range from 3.5 to 4.1 years (Dean and Schrenk, 2003). Data on fossil orangutan molar crown development presented here reveal an even more prolonged developmental pattern than in living or fossil apes, thus similarities between living orangutans and Miocene apes are likely to be an evolutionary convergence, as is the case with aspects of tooth structure and dental development in living orangutans and modern human.

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Appendix. Molar crown formation times (in days) for living orangutan presented by species and sex.

Taxon	Sex	Tooth	Cusp	n	Mean (range)
<i>P. pygmaeus</i>	n/a	UM1	mb	1	1060
			ml	1	1028
		LM1	mb	1	1082
			ml	1	910
	F	UM1	mb	2	1075 (1006–1144)
			ml	1	1210
			db	1	1044
			dl	2	1170 (1086–1254)
		UM2	mb	1	1146
			ml	2	1274 (1213–1336)
			db	1	1203
		UM3	mb	2	1133 (1064–1202)
			ml	1	1092
		LM1	mb	1	1304
			ml	1	807
		LM2	dl	2	830 (764–896)
			mb	2	1333 (1272–1394)
		LM3	dl	1	833
			mb	1	1469
	M	UM2	mb	1	1058
			ml	1	1265
		LM1	dl	1	986
			ml	1	1003
		LM2	dl	1	895
			ml	1	1000
		LM3	dl	1	1000
			ml	1	1046
	n/a	UM1	mb	1	1405
			ml	1	1318
		LM1	db	1	1046
			mb	1	1325
		LM2	ml	1	1069
			ml	1	1098
		UM2	dl	1	1457
			dl	1	1046
	F	LM1	mb	1	1794
			dl	1	1427
Captive <i>Pongo</i>	n/a	LM3	dl	1	900
			db	1	1544
	M ^a	UM3	db	1	1698
			mb	1	1421
		LM1	db	1	1489
			dl	1	1374
		LM2	dl	1	1374
			dl	1	1141
		LM3	dl	1	1141
			dl	1	1141

n/a = sex unknown, F = female, M = male, U = upper/maxillary, L = lower/mandibular, M = molar, mb = mesiobuccal, ml = mesiolingual, db = distobuccal, dl = distolingual.

^a Originally studied by Beynon et al. (1991a).

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